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Unique nesting biology of *Osmia* (*Melanosmia*) *uncinata*, a Palaearctic osmiine bee specialized on thick-barked conifers (Hymenoptera, Megachilidae)

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Abstract

Osmia (*Melanosmia*) *uncinata* Gerstäcker is a Palaearctic megachilid bee distributed from temperate and northern Europe eastwards to the Russian Far East. The discovery of over 80 nests in Switzerland, southern Germany and Scotland enabled for the first time a closer investigation of its nesting biology and prompted the assessment of the species' phenology, distribution and habitat. *O. uncinata* nested in self-excavated burrows inside the bark of both living trunks and dead stumps of *Pinus sylvestris*. The nests were excavated at a height of 10–220 cm above ground either on the underside of prominences of longitudinal bark ribs or inside beetle borings and extended more or less vertically upwards. They consisted of a single straight to slightly curved burrow with rarely one to three side burrows, had a total length of 1.2–12.0 cm and contained 1–6 brood cells. The brood cells, which faced downwards with the larval provisions being located in the upper cell half, were separated from each other by one-layered walls of chewed leaves ("leaf pulp"). The nests were sealed with a plug of 2–4 closely adjacent walls of leaf pulp. DNA metabarcoding of cell and plug walls revealed that *Potentilla* and *Fragaria* (Rosaceae) served as leaf pulp sources. Pre-imaginal mortality amounted to 77%, partly caused by brood parasites such as *Sapyga similis* (Sapygidae) and *Cacoxenus indagator* (Drosophilidae) or predators such as snakeflies (Raphidioptera). At low elevations, *O. uncinata* needs one year for its development and overwinters as imago inside the nest, whereas in the subalpine zone of the Alps it has a two-year cycle passing the first winter as prepupa and the second winter as imago. *O. uncinata* starts to emerge between the end of March at low elevations and the end of May at higher elevations qualifying as an early flying bee like the other European *O.* (*Melanosmia*) species. The distribution of *O. uncinata* in Central Europe and Scotland largely coincides with the occurrence of *P. sylvestris*. As in the pine, it extends over a wide altitudinal range from below 100 m up to 1900 m a.s.l. and encompasses dry and wet as well as warm and cold habitats including open pine forests, inner and outer forest edges dominated by pine and isolated pine groups. At a few locations in the subalpine zone of the Alps, *O. uncinata* occurs in the absence of *P. sylvestris*; here, the thick bark of *Larix decidua* serves as a substitute nesting substrate.

Key Words

Anthophila, Apiformes, mandibular strength, Osmiini, *Rhagium*, X-raying

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Introduction

Osmia uncinata Gerstäcker (Megachilidae, Osmiini) is a Palaearctic mason bee of 8–10 mm body length that is usually found in or near forests (Figs 1–4). The females collect pollen mainly on *Hippocrepis*, *Lotus* and other Fabaceae species, although representatives of more than ten other plant families also serve as pollen hosts (Müller 2018; Westrich 2018). *O. uncinata* is a member of the large Holarctic subgenus *Melanosmia* Schmiedeknecht, which is represented in Europe by 12 mostly cold-adapted and mountainous species often exhibiting an arctoalpine or boreomontane distribution (Rightmyer et al. 2010, Müller 2020). The females of many *O.* (*Melanosmia*) species are morphologically very similar and difficult to identify. Information on the biology of *O.* (*Melanosmia*) species in the older literature should therefore be treated with caution. In fact, *O.* (*Melanosmia*) *pilicornis* Smith was formerly assumed to nest in stony ground, in empty snail shells, under loose bark or in insect burrows in dead wood until it finally turned out that the species obligatorily gnaws its nests in dead fallen branches of trees (Lemoine 2016; Prosi et al. 2016). Similarly, *O.* (*Melanosmia*) *nigriventris* (Zetterstedt) was repeatedly hypothesized to nest in insect burrows in dead wood, which was found to be erroneous by a recent study showing that it actually excavates its nests mainly in pieces of larch and pine bark lying on the ground (Müller et al. 2019).

Published information on the nesting biology also exists for *O. uncinata*, although no nests have ever been described in detail. The species was reported to construct its brood cells in old tree stumps (Friese 1891), in the bark of pine trees (Bouwman 1922; Stoeckhert 1933; Willems 2010), in burrows of the cerambycid beetle *Rhagium inquisitor* L. (Edwards 2001; Else and Edwards 1996, 2018; Taylor 2015) or in drilled borings of wooden trap nest blocks (Westrich in Else and Edwards 2018). However, the hypothesized use of insect burrows in dead wood as nesting site raises doubts. First, compared with other representatives of *O.* (*Melanosmia*) the mandibles of *O. uncinata* females are considerably stronger than those of species that nest in pre-existing cavities or loose soil but weaker than those of species that are capable of tunneling out their nests in hard wood (Müller et al. 2019). Second, numerous attempts to establish *O. uncinata* in trap

Figures 1–4. *Osmia uncinata*. **1)** Female on *Lotus corniculatus* (Fabaceae). **2)** Female on *Rubus* spec. (Rosaceae; photo A. Jacobs). **3)** Male. **4)** Female at the entrance of her nest.

nests composed of cardboard tubes or drilled borings in dead wood all have failed (Taylor 2011; Sears et al. 2014; A. Müller and R. Prosi unpublished). Third, the distribution of *O. uncinata* in Central Europe appears to be very patchy coinciding neither with a certain altitude nor with overall forest cover. These findings all point to a more specialized nesting biology than hitherto assumed.

In spring 2019, we discovered in an open pine forest in eastern Switzerland near Trimmis (Grisons) a strongly weathered linear burrow on the surface of the bark of a healthy pine (*Pinus sylvestris* L.) about one meter above the ground (similar to Fig. 16). This burrow, which was 3.2 cm long, 5 mm wide and directed vertically upwards, had undoubtedly been gnawed out by an insect and most probably run completely inside the bark at the time of its creation. Indeed, an almost identical burrow was found in the bark of a neighbouring pine tree, which was entirely hidden and ran several millimeters below the bark surface. Interestingly, this second burrow contained remains of brood cell partitions built from chewed green leaves ("leaf pulp"), most probably originating from an osmiine bee. As *O. uncinata* was recorded in the same pine forest, the suspicion arose that these two burrows could be old nests of this bee species. This suspicion was later confirmed by the systematic examination of the bark of numerous *P. sylvestris* trees at eight different localities in Switzerland and southern Germany, which revealed many old and few new nests, some of which contained dead or living imagines of *O. uncinata*.

In the present publication we describe nesting site, nest architecture and brood parasites of *O. uncinata* based on 80 nests and compare these Central European nests with two nests recently found in northern Scotland (Taylor 2015). Furthermore, we identify the nest building material by DNA analysis of nest closures and brood cell partitions, characterize the phenology and habitat of *O. uncinata* in Central Europe and present a distribution map of the species' range.

Methods

Between spring and winter 2019, the bark of *Pinus sylvestris* trees was checked for nests of *Osmia uncinata* at seven sites in eastern and northern Switzerland and at one site in southern Germany, where the species was known to occur: Sent/Grisons (46°48'45"N, 10°21'36"E; 1100 m a.s.l.), Versam/Grisons (46°48'28"N, 9°20'03"E; 650 m a.s.l.), Trimmis/Grisons (46°53'23"N, 9°33'50"E; 750 m a.s.l.), Lommis/Thurgau (47°31'32"N, 8°58'51"E; 550 m a.s.l.), Hüntwangen/Zurich (47°35'21"N, 8°30'55"E; 400 m a.s.l.), Beringen/Schaffhausen (47°42'03"N, 8°35'37"E; 550 m a.s.l.), Merishausen/Schaffhausen (47°46'22"N, 8°36'42"E; 650 m a.s.l.) and Immendingen/Baden-Wuerttemberg (47°55'56"N, 8°41'39"E; 700 m a.s.l.). At each site, both trunks and stumps of *P. sylvestris* were systematically examined from the ground up to a height of about 2.25 m with the aid of a torch and a pocket mirror, which facilitated the discovery of nest entrances hidden in bark cracks, fissures or ruptures. Bark areas containing potential nests as suggested by open circular holes of 4–5 mm in diameter, by nest plugs built from leaf pulp or by more or less exposed vertical burrows of 4–5 mm width were cut out and transported back to the lab. Old nests were directly dissected with a pocket knife, whereas new nests sealed with a nest plug were X-rayed first at the Vetsuisse Faculty of the University of Zurich using both a Bucky Diagnost CS/TH X-Ray (Philips) combined with a Profect CS Mammo-Reader (Fujifilm) and an ultra-high resolution digital radiography system (UltraFocus 100, Faxitron), before they were opened. In addition, a piece of bark from a burnt *Pinus sylvestris* stump in northern Scotland near Aviemore (57°11'43"N, 3°49'26"W; 220 m a.s.l.), which contained two nests of *O. uncinata* built within beetle borings of *Rhagium inquisitor* (Cerambycidae), was X-rayed. These nests were discovered by Gus Jones and described by Taylor (2015). In April 2020, the bark of trunks and stumps of *Larix decidua* Miller in a subalpine larch forest near Blatten in the Lötschental/Valais (46°25'20"N, 7°49'00"E; 1600–1800 m a.s.l.) was examined for nests in close vicinity of recent *O. uncinata* sightings.

To identify the source of the nest building material used by *O. uncinata*, DNA metabarcoding of nest plugs and brood cell walls consisting of leaf pulp was performed by Eurofins Medigenomix GmbH (Ebersberg, Germany). The leaf pulp material used for DNA analysis originated from two nests discovered in Lommis (2 cell walls) and Immendingen (3 plug and 3 cell walls). DNA of each of the two samples was extracted with the Maxwell 16 FFS nucleic acid extraction kit (Promega) following the manufacturer's manual. From the extracted DNA, barcoding sequences of the nuclear marker ITS2 and the chloroplast marker trnL were PCR amplified using target specific next-generation sequencing primers and analysed by amplicon sequencing on the Illumina MiSeq platform. The amplified sequences were sorted into sequence clusters according to their similarity, each represented by a master sequence. The master sequences were identified to species or genus level by comparing them with known plant sequences made available by the NCBI database.

To clarify the phenology and distribution of *O. uncinata*, we conducted a comprehensive literature survey, gathered unpublished records from public and private entomological collections and retrieved distributional data from several public databases (for details see Acknowledgments and Suppl. material 1, which contains a complete list of all distributional data). For the phenology, only records from Central Europe (Austria, Czech Republic, French Alps, Germany, Italian Alps, Liechtenstein, Poland, Slovakia, Slovenian Alps and Switzerland) were considered.

To examine whether the distribution of *O. uncinata* is confined to stands of *P. sylvestris*, we applied three methods. First, we compared the Swiss records of *O. uncinata* (n = 198) with those of *P. sylvestris* using the open-source

geographic information system QGIS, version 3.4 (www.qgis.org). These records were made available by the Centre Suisse de Cartographie de la Faune (CSCF) for *O. uncinata* and the Swiss National Forest Inventory carried out by the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) for *P. sylvestris* (WSL 2019). Second, we checked each square kilometre of the Swisstopo grid (www.swisstopo.admin.ch), for which records of *O. uncinata* were known (n = 172), for the presence of *P. sylvestris* stands ("pine presence") by the following step-wise procedure: i) analysis of aerial photos provided by the Swiss mapping platform (https://map.geo.admin.ch); if the occurrence of *P. sylvestris* stands was uncertain after the aerial photo analysis, ii) we contacted the appropriate bee recorder or forest official; if the presence of *P. sylvestris* stands was still unclear, iii) we checked the square kilometre in the field. Pine presence was differently defined depending on the precision of the bee record: if the record was precise to the nearest 250 m, pine presence was assumed when there were pine stands in a radius of 250 m around the record; if the record was less precise, pine presence was assumed when there were pine stands within the square kilometre. Third, we made a survey among German and Austrian bee experts asking them to judge the presence of *P. sylvestris* stands in a radius of 250 m around each of their own *O. uncinata* records according to the following three categories: i) presence of *P. sylvestris* stands certain or highly probable, ii) absence of *P. sylvestris* stands certain or highly probable, iii) presence of *P. sylvestris* stands unclear.

Results

Nesting biology

Nesting site

Nests of *Osmia uncinata* were found at each of the eight study sites. In total, 80 nests were discovered, 71 of which were abandoned and one to several years old, whereas nine were new containing living or freshly dead progeny (n = 8) or an adult female, which had died within her first unfinished brood cell for unknown reasons (n = 1). All nests were built inside the outermost bark layer of trunks of living and healthy trees of *Pinus sylvestris*, which grew at sunny places of open pine stands (Figs 5–10). The trunk diameter at breast height of trees selected as nesting sites varied from 16–76 cm (Fig. 15a). All nest entrances, which were circular in shape and had a diameter of 4.25–4.75 mm, were located below 1–3 cm thick prominences of longitudinal bark ribs and were visible only from below (Figs 4, 11–14, 17). The only exception was a single nest that entered the bark on the lateral side of a rib. The nest entrances were at a height of 16–220 cm above the ground (Fig. 15b). As the bark of pine trunks usually becomes considerably thinner at heights between two and three metres offering increasingly less suitable nesting sites, the proportion of overlooked nests higher than two metres above the ground is expected to be low. The bark areas containing nests were exposed in all directions (Fig. 15c). However, most of the nests were located on the east, southeast, south and southwest side of the trunks, whereas a much smaller proportion was on the less sun-exposed trunk areas.

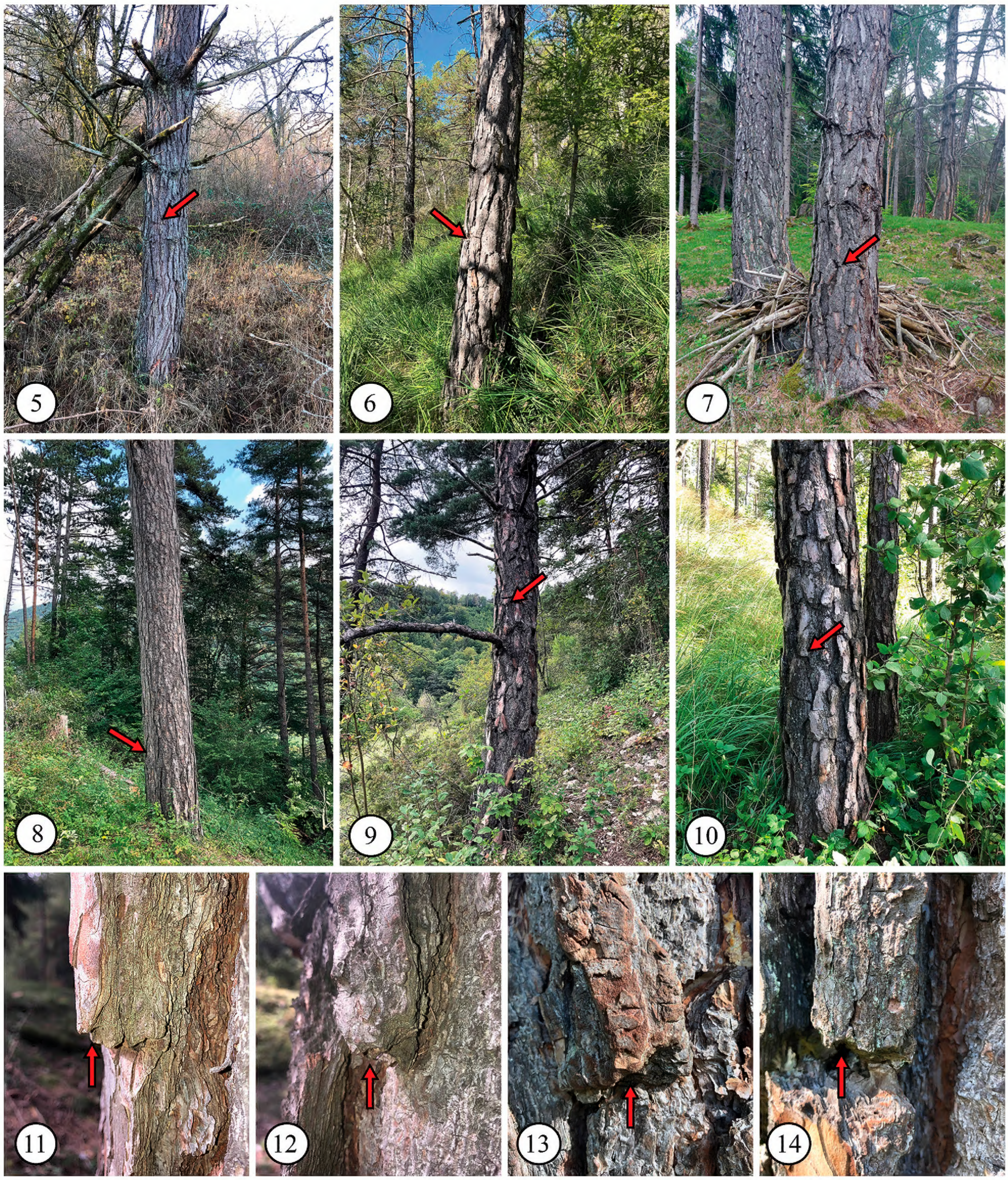
The nesting site described above corresponds to the behaviour of three females of *O. uncinata*, which examined the bark of *Pinus sylvestris* while searching for a suitable nesting place near Trimmis on 8.6.2019. One female checked the bark of a dead pine stump, while the others patrolled the bark of living pine trunks. The latter two females started their search at the base of the tree and flew slowly along the sunny side of the trunk up to a height of 1.5–2.5 m, before they left and flew to the base of a neighbouring pine tree to start a new upwardly search flight. All three females repeatedly interrupted their flight and landed on the bark to carefully inspect fissures, fractures and prominences. The same behaviour was observed in two females of the sapygid wasp *Sapyga similis* (Fabricius), which examined the pine bark most probably in search for nests of their host *O. uncinata* (see below). Host-nest searching females of *S. similis* at the bark of old pine trees were also reported by Tischendorf (2002).

Three nests containing living progeny or freshly dead adults at the time of their discovery were most likely reused as indicated by the presence of at least one year old remains of leaf pulp walls. Whether such nests were enlarged in the year of reuse by prolonging the main burrow or by excavating side burrows is unclear. Other aculeate Hymenoptera also used the abandoned nesting burrows of *O. uncinata* to place their brood cells, such as *Heriades*, e.g. *H. truncorum* L. (Megachilidae, n = 1), *Hylaeus*, e.g. *H. communis* Nylander (Colletidae, n = 11), *Passaloecus*, e.g. *P. eremita* Kohl (Crabronidae, n = 2), *Trypoxylon* (Crabronidae, n = 1), *Deuteragenia* (Pompilidae, n = 2) and eumenine wasps (Vespidae, n = 1); in five other reused nests with remains of earthen cell walls the owner could not be identified.

Nest architecture

The nests were all tunneled out by the females of *Osmia uncinata* with no indication that pre-existing burrows e.g. of cerambycid beetle larvae were used. The nesting burrows were carefully carved out and measured mostly 4.25–4.75 mm in diameter (range 4.0–5.75 mm). They were neither lined with glandular secretions nor with leaf pulp except sometimes for small areas of a few square millimetres covered with a thin layer of leaf pulp, which was probably applied to smooth out irregularities or to fill small cracks. The burrows, which were completely hidden 2–13 mm below the bark surface, ran more or less vertically upwards and parallel to the trunk surface (Figs 16, 18–25).

The nests usually consisted of a single straight to slightly curved burrow of 1.3–8.0 cm length (n = 63; Figs 15d, 16, 18–22). In eight nests, however, one (n = 5),



Figures 5–14. Nesting site of *Osmia uncinata*. **5–10)** Position of nests in the bark of *Pinus sylvestris* trunks. **11–14)** Nest entrances below prominences of longitudinal bark ribs.

two (n = 2) or three (n = 1) side burrows branched off the main burrow (Figs 23–25). These side burrows were excavated in the same plane as the main burrow and the longer ones ran parallel to the main burrow. The total length of nests with a main burrow and one to three side burrows varied from 4.7–12.0 cm (Fig. 15d).

The new nests as well as those old nests, for which the number of brood cells could properly be ascertained due to remains of cell partitions or dead bee progeny, contained 1–6 brood cells (Fig. 15e). The brood cells were constructed either singly in short burrows or in a linear series of 2–5 in longer burrows (Figs 28–30). They had a length of 7.5–11 mm including the outer cell partition, a width of 4.5–5.75 mm and were slightly broadened in the middle (n = 49). Given these brood cell dimensions, some old nests with a total burrow length exceeding 7–8 cm

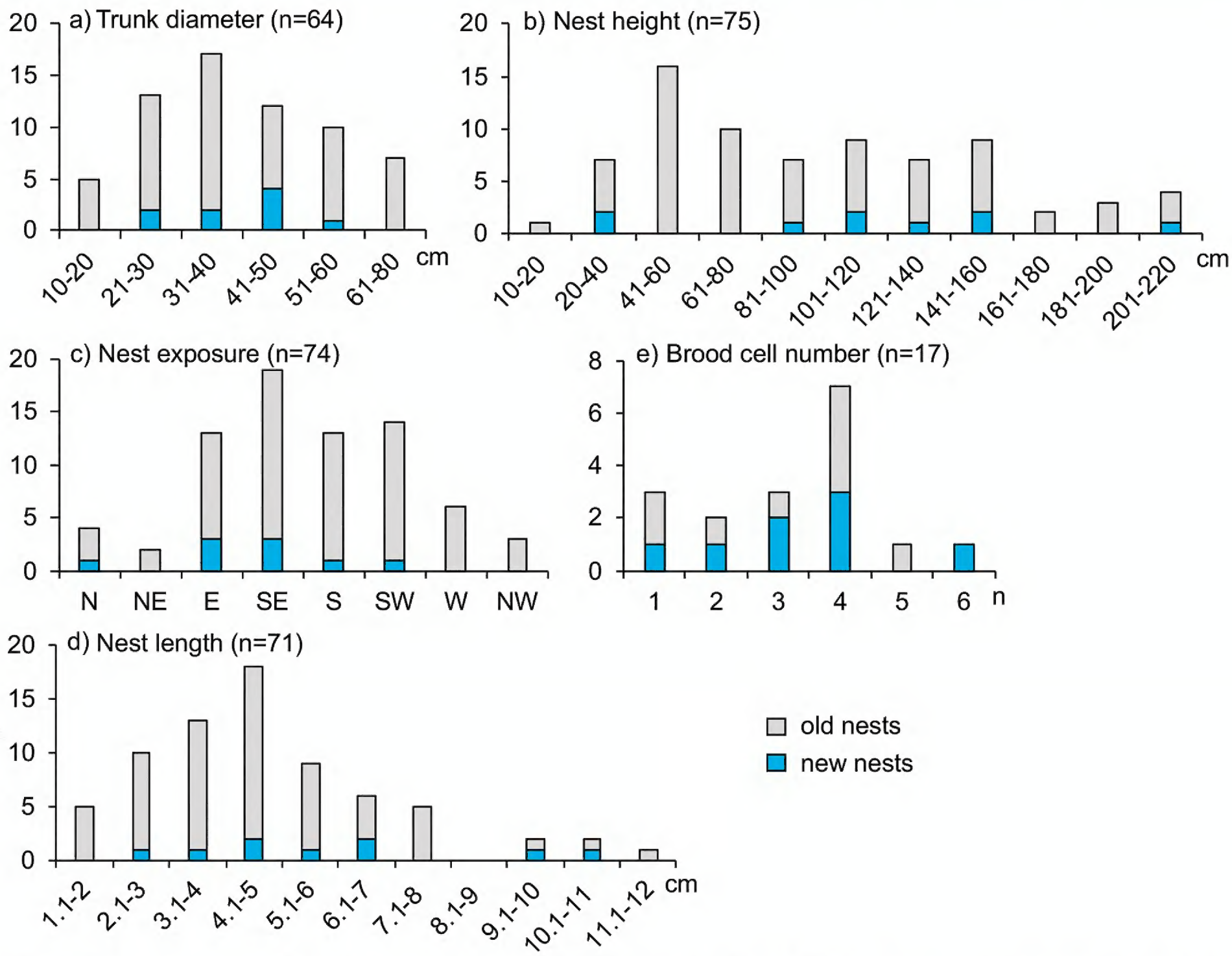


Figure 15. Nest parameters of *Osmia uncinata*. **a)** Trunk diameter at breast height of *Pinus sylvestris* trees selected as nesting site. **b)** Height of nest entrance above the ground. **c)** Exposure of nest. **d)** Length of nesting burrow. **e)** Number of brood cells. Grey = abandoned nests; blue = nests occupied upon discovery.

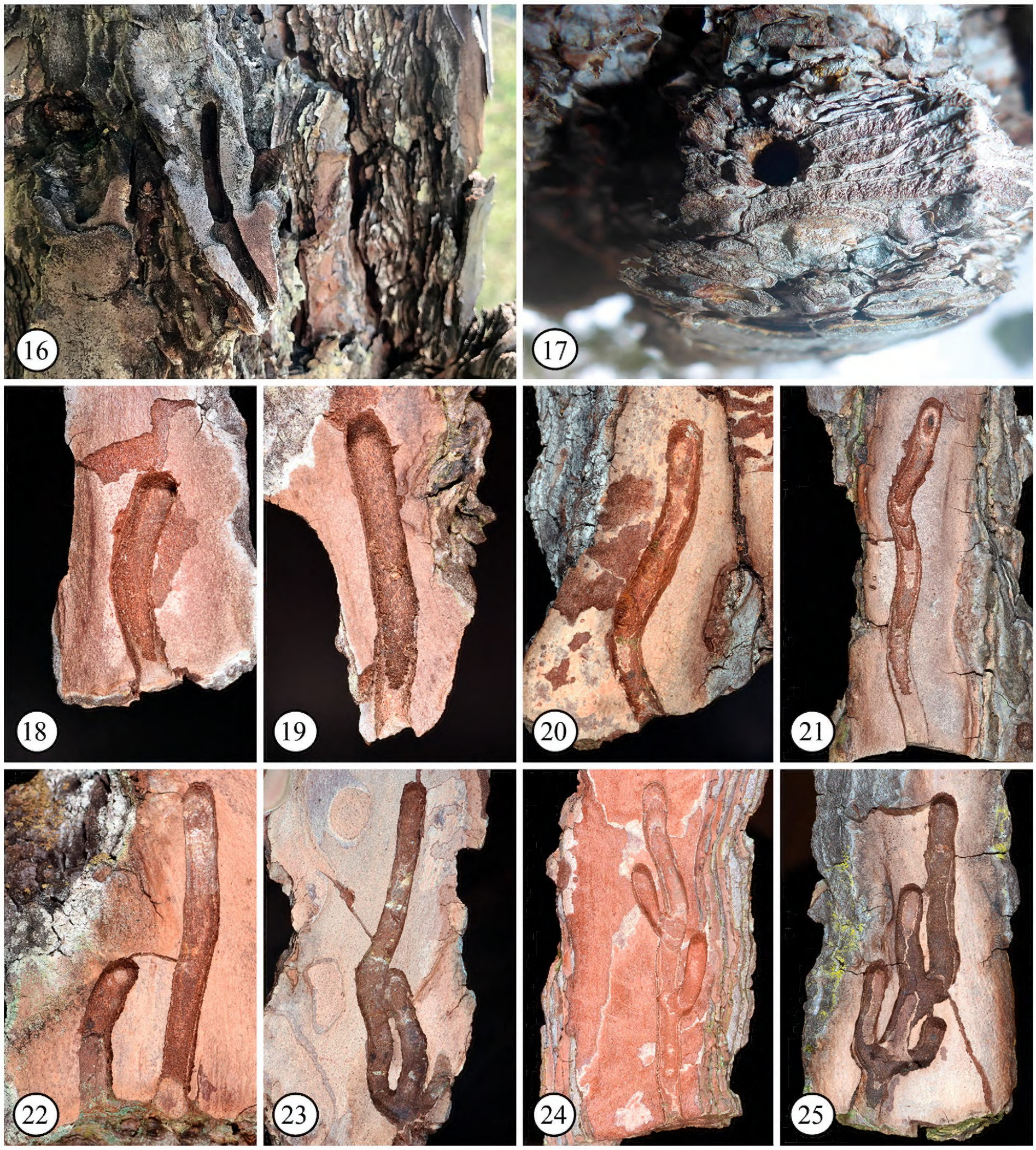
might possibly have contained more than six brood cells. In spite of the vertical orientation of the nesting burrows, the larval provisions were located in the basal, i.e. upper half of the brood cell (Figs 29, 30).

Each brood cell was sealed towards the nest entrance with a one-layered wall built from leaf pulp without addition of other material (Figs 28–30). These cell walls had a maximum marginal width of 1–2 mm and a minimum central width of 0.25–0.75 mm (n = 13). As revealed by a threshold of leaf pulp at the entrance of a still empty brood cell, the females mark the position of the later cell wall before they begin to provision the cell; this threshold was ring-shaped, which seems to be typical for *Osmia* species of the subgenus *Melanosmia* (Müller et al. 2019). Between the outermost cell wall and the innermost wall of the nest plug was an empty vestibule, which ranged in length from 2.75–11 mm (n = 7); in one exceptional case the vestibule was 22 mm long (Fig. 30). The nest plug, which measured 4–9 mm in total length (n = 8), consisted of two (n = 2), three (n = 5) or four (n = 1) one-layered walls made from leaf pulp (Figs 26–28, 30). These plug walls were constructed immediately behind each other, rarely enclosing a few loose clumps of leaf pulp between them. They were thicker than the cell walls and had a maximum marginal width of 1.5–3.5 mm and a minimum central width of 0.5–1.25 mm (n = 23). The outermost plug wall was either flush with the nest opening (n = 3) or slightly recessed by 1–3 mm (n = 3); in two reused nests, it was at a distance of 1.0 cm and 2.1 cm from the opening.

DNA metabarcoding revealed that the brood cell and plug walls of two nests were constructed from masticated leaves of *Fragaria* spec. and *Potentilla* spec. (both Rosaceae) (Tab. 1). In addition, very low proportions of sequence reads corresponded to Asteraceae and *Viola* (Violaceae). Although the percentage of reads obtained by

Table 1. Origin of the masticated green leaves used by *Osmia uncinata* to build the walls of brood cells and nest plugs based on DNA metabarcoding of a sample of eight walls of two nests originating from two localities in Switzerland and southern Germany.

Locality	Plant taxon	% sequence reads
Lommis/Thurgau (1 nest, 2 walls)	*Fragaria* spec.	100
Immendingen/Baden-Wuerttemberg (1 nest, 6 walls)	*Fragaria* spec.	77.2
	Potentilla spec.	17.6
	Asteraceae spec.	2.7
	Viola spec.	2.5

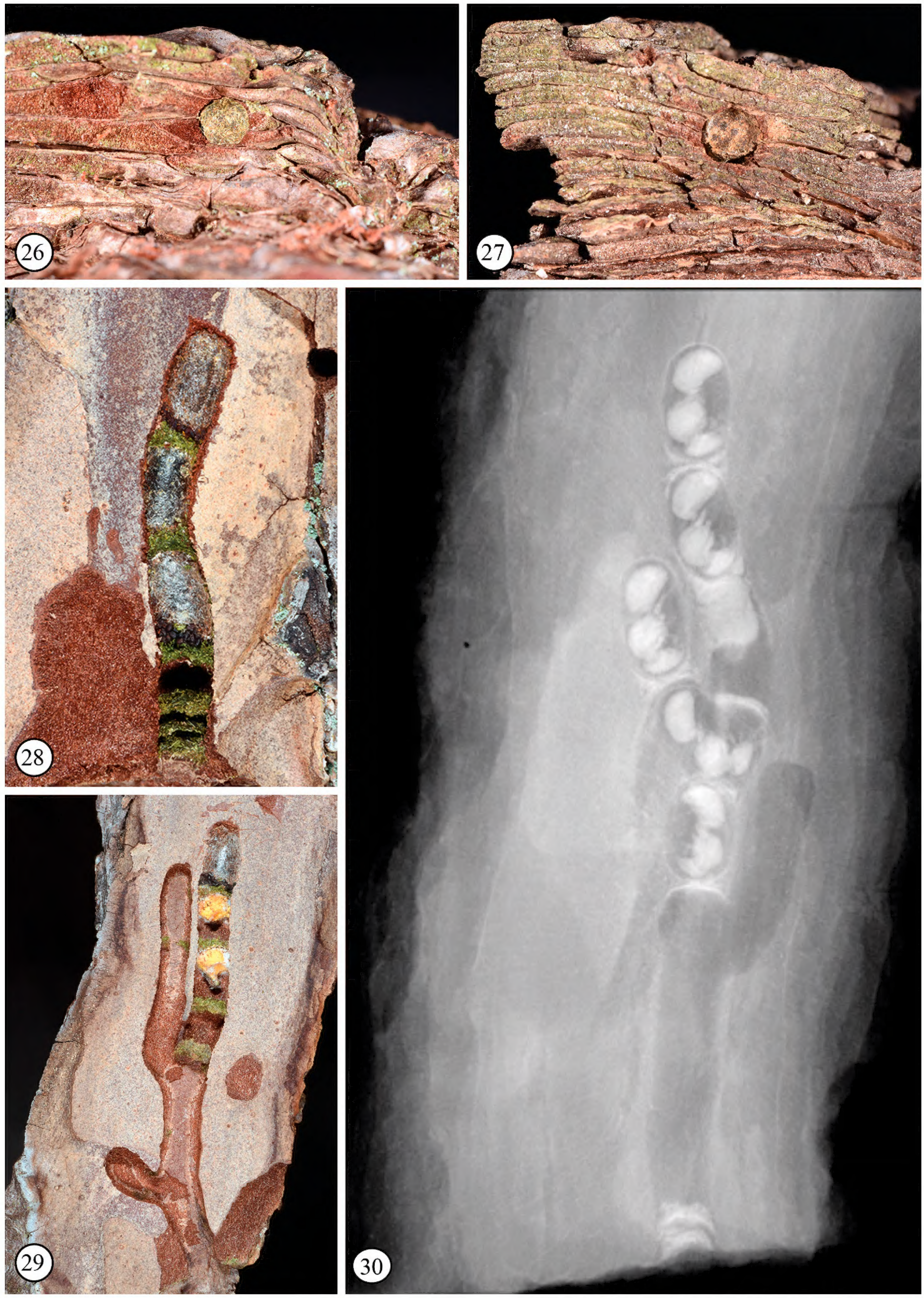


Figures 16–25. Nest architecture of *Osmia uncinata*. **16)** Several years old nest after uppermost bark layer has flaked off. **17)** Entrance to old nest seen from below. **18–25)** Dissected nests consisting of a single burrow (**18–22**) or of one to three side burrows branching off the main burrow (**23–25**).

next-generation sequencing is only a rough indication for the relative amount of a plant taxon in the extracted DNA, this low proportions might be due to contaminations.

Larval mortality

Osmia uncinata successfully developed to the imaginal stage only in two of the eight nests that were occupied upon discovery: a three-celled nest produced one male and a six-celled nest produced four females and one male (Fig. 30). In five brood cells of four nests, two females and three males of the sapygid wasp *Sapyga similis* (Fabricius) developed. Three adjacent cells within the same nest were destroyed by the drosophilid fly *Cacoxenus indagator* Loew. The content of two neighbouring cells within the same nest was devoured by the larva of a snakefly (Raphidioptera). And in ten cells distributed among four nests the larvae of *O. uncinata* died for un-

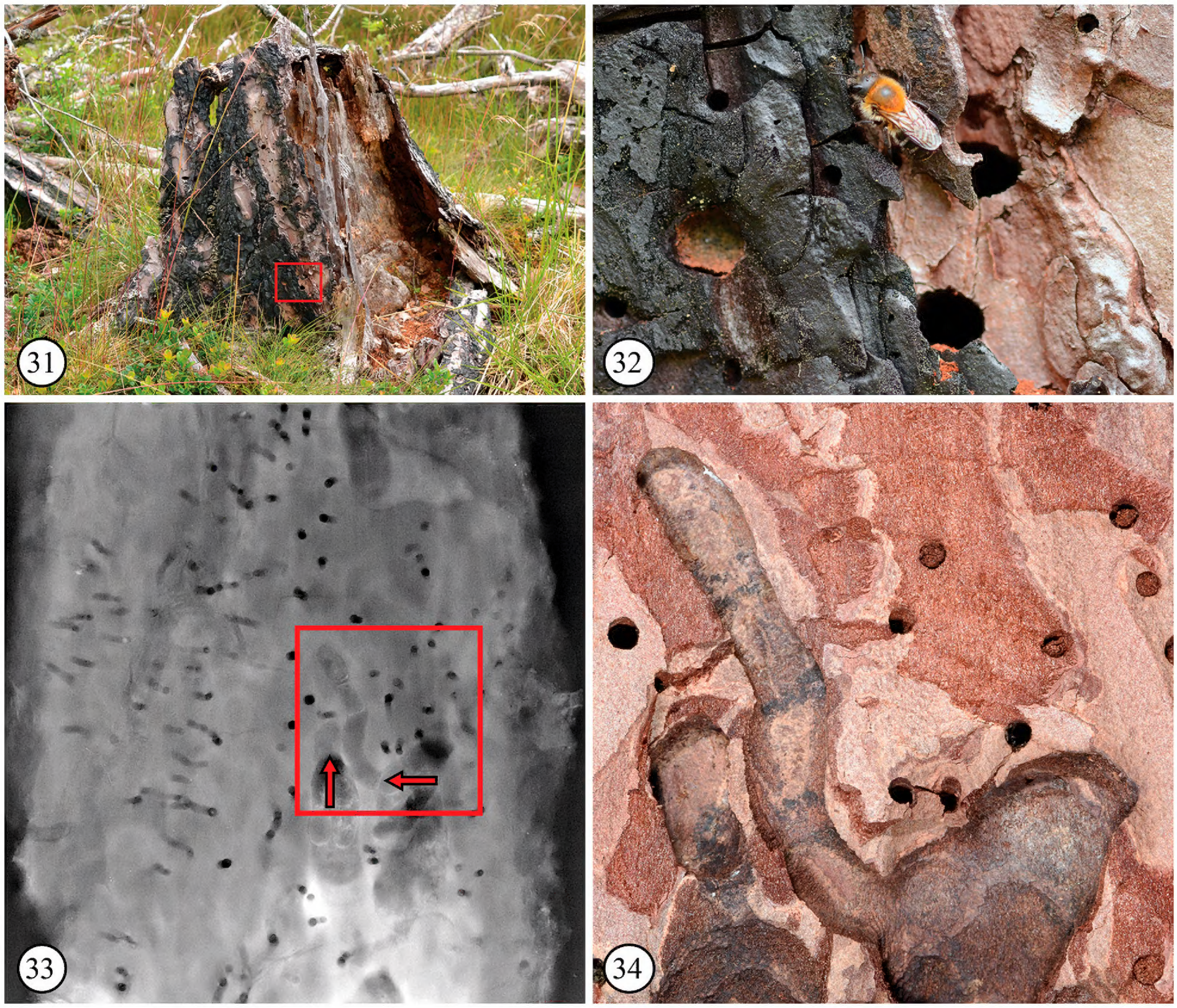


Figures 26–30. Nests of *Osmia uncinata*. **26–27)** Nest entrances sealed with leaf pulp. **28)** Dissected nest with three brood cells each containing a cocoon. **29)** Dissected unfinished nest with cocoon in uppermost cell and dead larva on food provision in two cells. **30)** X-rayed nest with six cells containing four overwintering females, one overwintering male (outermost cell) and a dead larva on food provision.

known reasons. In summary, a successful development of *O. uncinata* failed in 20 out of 26 brood cells, which corresponds to a pre-imaginal mortality of 77%.

The Scottish nests

The two nests of *Osmia uncinata* discovered in the Scottish Highlands were located inside the bark of a *Pinus sylvestris* stump (Fig. 31). They were constructed by the same female, which entered each nest by an exit hole of the xylophagous beetle species *Rhagium inquisitor* L. (Cerambycidae). The two exit holes lay 10 cm and 11 cm above the ground and were separated by a distance of less than 5 cm (Figs 31, 32). Upon discovery, one nest had been sealed by the female bee with leaf pulp (nest 1), whereas the other was being provisioned (nest 2). Each nest consisted of a 4.5–5 mm wide burrow, which had a length of 1.2 cm in nest 1 and 4.0 cm in nest 2 (Figs 33, 34). The two nesting burrows were tunneled out by the female at the roof (nest 1) or the upper lateral corner (nest 2) of the beetle boring. Both were directed upwards and they contained one (nest 1) and three (nest 2) brood cells. The presence of numerous small borings of anobiid beetles – probably *Ernobius mollis* (L.) – in the bark directly above the *Rhagium* exit areas was likely the reason why the short nesting burrow of nest 1 was not advanced further upwards and why the burrow of nest 2 was started laterally rather than apically within the beetle boring (Figs 33, 34). Nest 1 was sealed with walls of leaf pulp both at the entrance of the short nesting burrow and



Figures 31–34. Scottish nests of *Osmia uncinata*. **31)** Stump of a burnt *Pinus sylvestris* tree containing two nests. **32)** Female of *O. uncinata* on bark with three large exit holes of *Rhagium inquisitor*, of which the upper two served as entrance to one nest each: nest 1 (left) is sealed, nest 2 (upper right) is being provisioned; note the bark particles that have accumulated below nest 2, indicating the former digging activity of the female. **33, 34)** X-rayed bark (left) and dissected nests (right) with nest 1 excavated at the roof and nest 2 excavated at the upper lateral corner of the *Rhagium* boring; the large dark spots on 33) are the three *Rhagium* exit holes, the numerous small spots are exit holes of anobiid beetles. The red arrows indicate the entrance to the excavated nesting burrows and the red frames the enlarged section on the opposite image.

at the opening of the *Rhagium* boring at the bark surface. Nest 2 remained unsealed, probably because the female died before the last brood cell was finalized.

Nests in the Lötschental/Valais

In the subalpine larch forest searched for nests of *Osmia uncinata*, three abandoned nests and one new nest were discovered in the bark of living trees of *Larix decidua*, which grew at an altitude between 1630–1780 m a.s.l. and measured 61–79 cm in trunk diameter. The nest entrances were 77–146 cm above the ground and – as in the nests in pine bark – were situated below prominences of longitudinal bark ribs. The four nests were located on the south (n = 2) and southeast (n = 2) side of the trunks. Their architecture exactly corresponded to that of the nests in pine bark described above. The new nest contained two brood cells with an overwintering prepupa each of *Sapyga* spec. and *O. uncinata*.

Phenology and overwintering stage

In Central Europe, the imaginal period of *Osmia uncinata* varies depending on the altitude (Fig. 35, Suppl. material 1). At the lowest elevations below 500 m a.s.l., the flight activity may start already at the end of March and rarely extends beyond the end of June, whereas at elevations above 1500 m a.s.l. in the subalpine zone of the Alps the imagines usually do not emerge before mid June and normally fly till the end of July.

Six brood cells originating from two nests built in 2019 at an altitude of 550 m and 700 m a.s.l. contained living adults when they were opened in fall (Fig. 30), indicating that *O. uncinata* has a one-year cycle at lower elevations and overwinters as fully developed imago within the nest. In contrast, a brood cell in a nest built in 2019 at an altitude of 1630 m a.s.l contained a prepupa of *O. uncinata* in April 2020, suggesting that *O. uncinata* passes at least its first winter in the prepupal stage in the subalpine zone of the Alps (see Discussion).

Distribution and habitat

Osmia uncinata has a vast distribution occurring from temperate and northern Europe eastwards to the Russian Far East (Fig. 36). It inhabits a wide belt between 43° and 70° northern latitude, extending from 5° western to 153° eastern longitude. It is distributed from sea level up to about 1900 m a.s.l., with most records above 1500 m a.s.l. being situated in the inner alpine valleys of the Valais, Grisons and South Tyrol. It has been recorded from western Europe (Scotland, Belgium, Netherlands,

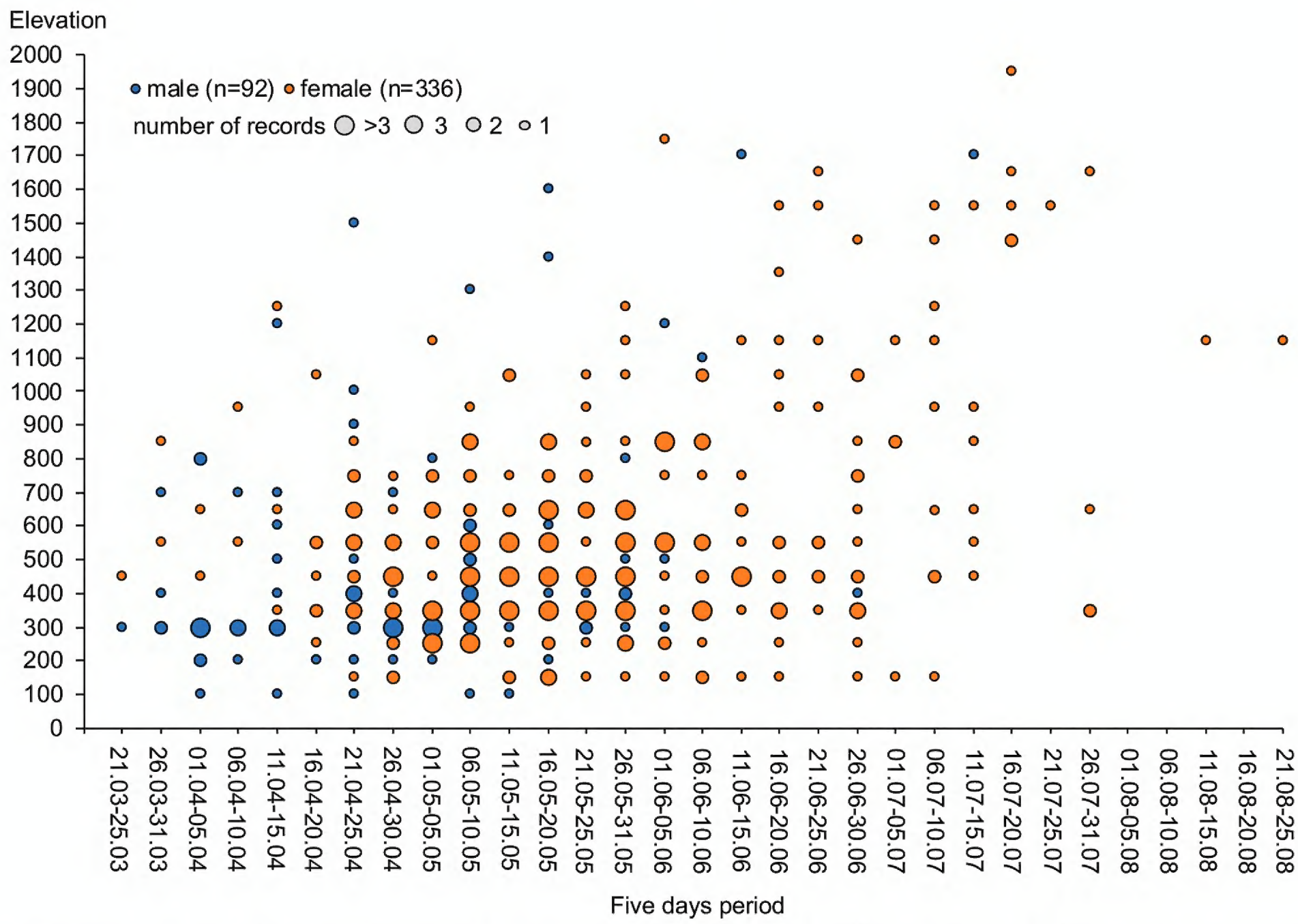


Figure 35. Phenology of *Osmia uncinata* in Central Europe. For each period of five days, the number of female and male records per elevation is given. For a given locality and date, only one record per sex was considered.

Figure 36. Distribution of *Osmia uncinata*. See Suppl. material 1 for a complete list of all distributional data. Made with Natural Earth (www.naturalearthdata.com).

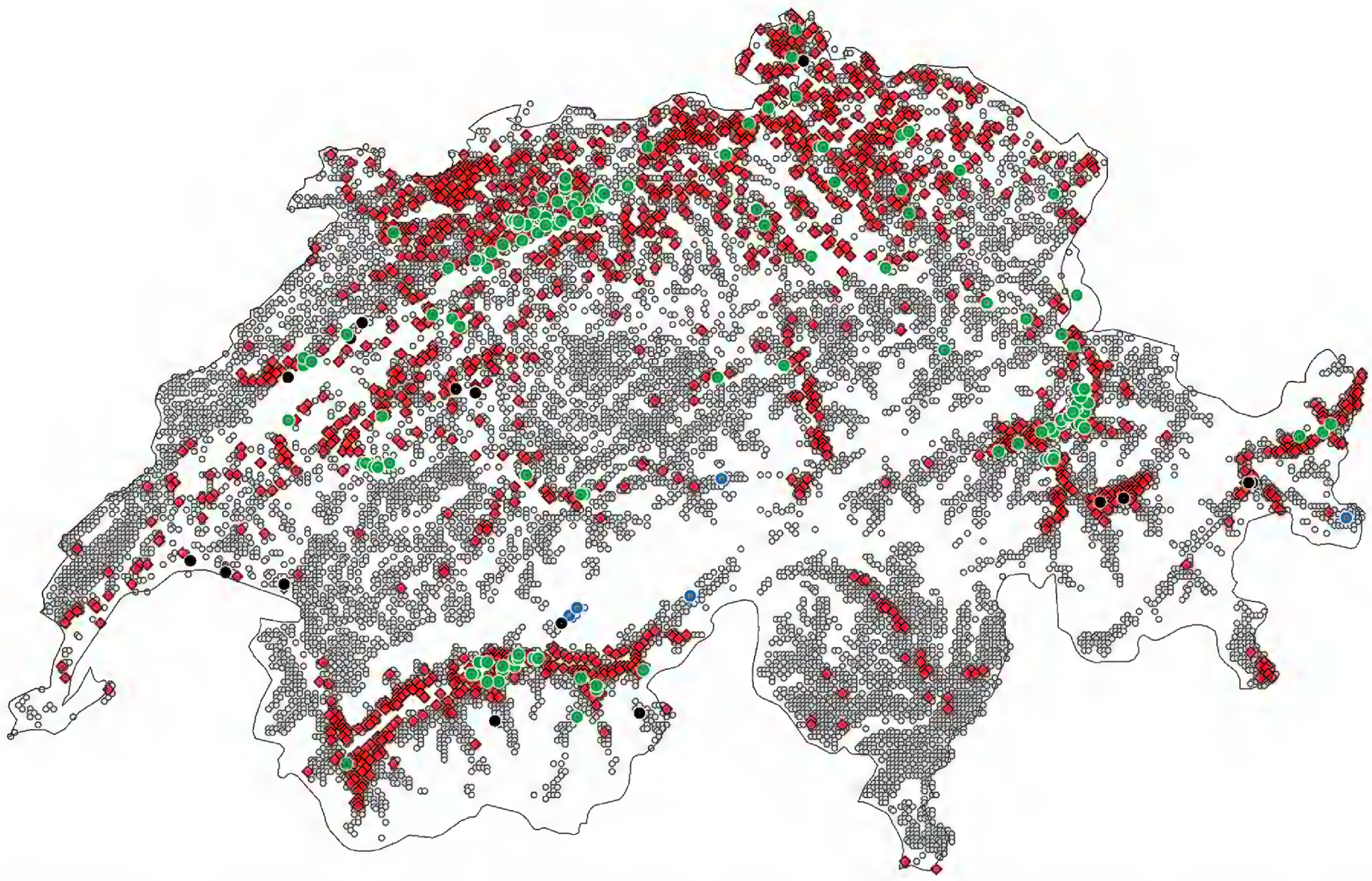


Figure 37. Swiss records of *Osmia uncinata* (n = 198) mapped onto the distribution of *Pinus sylvestris* in Switzerland. Grey = sample plots of the Swiss National Forest Inventory (NFI) without occurrence of *P. sylvestris*; red = sample plots of the NFI with occurrence of *P. sylvestris*; green = records of *O. uncinata* with pine presence; blue = records of *O. uncinata* without pine presence; black = records of *O. uncinata* not assignable to a square kilometre. Data made available by the Centre Suisse de Cartographie de la Faune (CSCF) for *O. uncinata* and the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) for *P. sylvestris* (WSL 2019).

Luxembourg, northern and southeastern France), central Europe (Switzerland, Liechtenstein, Germany, northern Italy, Slovenia, Austria, Czech Republic, Slovakia, Poland), northern Europe (Denmark, Norway, Sweden, Finland, Lithuania, Latvia, Estonia), eastern Europe (northern Ukraine, central and northern European Russia) and Asian Russia (Western Siberia, Eastern Siberia, Far East).

Mapping of the 198 Swiss records of *O. uncinata* onto the distribution of *Pinus sylvestris* in Switzerland revealed a distinct match between the occurrence of the bee species and the presence of pine stands (Fig. 37). Excep-

tions were few regions in the Valais (Lötschental, Obergoms), Bernese Oberland (Gadmental) and the Grisons (Val Müstair), where *O. uncinata* was recorded despite the lack of *P. sylvestris*. Out of the 198 Swiss *O. uncinata* records, 26 could not be assigned to a square kilometre and were excluded from the analysis of pine presence (see Methods). Among the remaining 172 records, pine presence was confirmed for 167 records (97.1%) and excluded for five records (2.9%). These five records originated from the Lötschental (Valais; n = 2), Obergoms (Valais; n = 1), Gadmental (Berne; n = 1) and Val Müstair (Grisons; n = 1) and were situated at elevations between 1500 and 1900 m a.s.l.. The identification of the bee individuals collected at these five localities proved to be correct with the exception of the Bernese record, which could not be confirmed as the specimen was not available. The presence of *P. sylvestris* in a radius of 250 m around the 70 records of *O. uncinata* reported by German and Austrian bee experts was certain or highly probable for 56 records (80.0%), highly improbable for one record (1.4%) and unclear for 13 records (18.6%).

Discussion

Nesting biology

Osmia uncinata nests in self-excavated short burrows in the outermost bark layer of *Pinus sylvestris* trees up to slightly more than two metres above the ground. Although all Central European nests were found in the bark of trunks of living trees, the observation of a female that examined the bark of a stump while searching for a suitable nesting site indicates that nests can also be tunneled out in the bark of stumps or dead trunks. In fact, the two nests of *O. uncinata* from Scotland were dug out in the bark of a burnt stump and Stoeckhert (1933) mentions pine stumps as nesting sites of *O. uncinata*. Based on the latter author, pieces of pine bark lying on the ground are occasionally also colonized. However, as *O. nigriventris* was found to occur at the very same locality, the nest mentioned by Stoeckhert most probably belonged to the latter species, which typically nests in detached bark pieces (Müller et al. 2019).

O. uncinata is one of the few osmiine bee species known to excavate its nests in wooden substrate. Among the Osmiini, such a behaviour appears to be restricted to *Osmia* species of the subgenus *Melanosmia* (Prosi et al. 2016). It only has been recorded so far in the Palaearctic *O. nigriventris* and *O. pilicornis* and in the Nearctic *O. bucephala* Cresson (Packard 1868; Prosi et al. 2016; Müller et al. 2019). The mandibles of *O. uncinata* females are considerably stronger than those of related Palaearctic *O.* (*Melanosmia*) species nesting in pre-existing cavities or loose soil, but distinctly weaker than those of *O. nigriventris* and *O. pilicornis* breeding in self-excavated burrows (Müller et al. 2019). The latter two species often excavate their nests in hard wood, which requires stronger mandibles than for tunneling out nests in relatively soft bark. Thus, the female mandibles of *O. uncinata* appear to be well adapted for gnawing in bark but are probably not strong enough to excavate nests in hard wood, supporting the assumption that *O. uncinata* is strictly specialized to bark for nesting.

The nesting burrows of *O. uncinata* were invariably oriented vertically upwards with the nest entrance situated at the lower end. Such an orientation is expected to be advantageous as rain runoff descending along the bark surface cannot enter the nest. Interestingly, *O. uncinata* positions its larval provisions in the upper half of the brood cell resulting in cells that face downwards. Downward-facing brood cells are known only in very few bee species (Danforth et al. 2019), e.g. in the Neotropic *Hylaeus tricolor* (Schrottky) (Colletidae), in the Palaearctic *Anthidiellum strigatum* (Panzer) (Megachilidae) and occasionally also in the Palaearctic *Heriades truncorum* (L.) (Megachilidae) (Sakagami and Zucchi 1978; Le Goff 2003; Westrich 2018). Why the provisions of these species do not run out of the brood cell during and after provisioning is unclear, but might be due to a combination of surface tension and viscosity (Danforth et al. 2019). As a consequence of the upper position of the provisions, the larvae are forced to feed in a hanging, upside down position making them susceptible to fall down to the cell bottom, from where they are hardly capable of reaching the provisions again.

Masticated green leaves of the two closely related genera *Fragaria* and *Potentilla* (Rosaceae) served as nest building material for *O. uncinata*. Both genera are also exploited by other *O.* (*Melanosmia*) species as leaf pulp sources, such as *O.* (*Melanosmia*) *nigriventris* and *O.* (*Melanosmia*) *pilicornis* (Prosi et al. 2016; Müller et al. 2019). This finding suggests that the selection of leaves for manufacturing leaf pulp might be far from accidental. In fact, several osmiine bee species belonging to the genus *Hoplitis* and to *Osmia* subgenera other than *Melanosmia* were also recorded to harvest leaf pulp from rosaceous genera, such as *Alchemilla*, *Fragaria*, *Potentilla*, *Rosa* and/or *Sanguisorba* (Müller and Richter 2018), supporting the view that the leaves of Rosaceae species might possess particularly favourable properties as nest building material. However, *O. uncinata* does not seem to be strictly specialized to Rosaceae for harvesting leaf pulp since a female was observed in the Netherlands biting off leaf material from *Betula pendula* Roth (Betulaceae) (Willems 2010).

The nests of *O. uncinata* discovered in the course of the present study rarely contained more than four brood cells, which is in line with Scottish nests found to contain one to three cells (Else and Edwards 2018, this study). As the females of osmiine bees usually lay from ten to 20 eggs during their lifetime under natural conditions (Raw 1972; Hawkins 1975; Correia 1981; Haeseler 1982; Müller 1994; Danforth et al. 2019), the females of *O. uncinata* are expected to build two or more nests during their flight period. The construction of few-celled nests might be a strategy to reduce the risk to lose all progeny after a brood parasite has detected a nest. In fact, the pre-imaginal mortality in 26 brood cells of eight nests of

O. uncinata amounted to 77%, which is unusually high for solitary bees (Minckley and Danforth 2019, but see Prosi et al. 2016 and Ivanov and Fateryga 2018). The high pressure exerted by brood parasites may not only explain the low number of brood cells per nest, but also why *O. uncinata* usually occurs in very low densities even at localities where there are many host flowers and numerous suitable nesting sites.

Contrary to the literature (Else and Edwards 1996, 2018; Edwards 2001), the Scottish females of *O. uncinata* do not place their brood cells in pre-existing beetle borings of *Rhagium inquisitor*. Instead, they use the *Rhagium* exit holes only to enter the bark before they excavate their own nest inside the bark. Thus, the only difference between the Central European and the Scottish nests of *O. uncinata* is that nest excavation started below bark prominences in the former and inside *Rhagium* borings in the latter. This difference is unlikely to be geographical but might rather be related to the thickness of the bark. We hypothesize that Central European females occasionally also enter the bark through exit holes of xylophagous beetles particularly when the bark lacks strong longitudinal ribs with transversal cracks, and that Scottish females sometimes also use the underside of bark prominences as starting point for excavating nests in case that the bark is thick enough.

Phenology and overwintering stage

Like other European representatives of the subgenus *Melanosmia*, which are early flying bees active in spring and early summer (Prosi et al. 2016; Westrich 2018; Müller et al. 2019), *Osmia uncinata* emerges in phenological spring, i.e. between the end of March at low altitudes and the end of May at higher altitudes. The overwintering of *O. uncinata* in the imaginal stage as found in the present study for elevations below 800 m a.s.l. is in line with this early flight period. In contrast to its one-year cycle at lower elevations, *O. uncinata* appears to need two years for its development in the subalpine zone of the Alps, where a nest at 1630 m a.s.l. still contained a prepupa in April. As the time span between the end of winter and the onset of the early flight period is hardly long enough at this altitude to allow for the metamorphosis to the imaginal stage, we hypothesize that *O. uncinata* passes the first winter as prepupa and the second winter as diapausing adult at higher elevations. Such an astonishing flexibility in adapting the duration of development depending on climatic conditions is also known from other osmiine bee species (Forrest et al. 2019).

Distribution and habitat

The range of *Osmia uncinata* in Central Europe largely coincides with the occurrence of *Pinus sylvestris* as revealed by the finding that pine presence was judged to be highly improbable for only a tiny fraction of the Swiss, German and Austrian *O. uncinata* records. The bee's distribution extends over a wide altitudinal range from below 100 m up to 1900 m a.s.l. and encompasses both dry and wet as well as both warm and cold habitats corresponding well to the distribution of *P. sylvestris*, which is characterized by a very wide ecological amplitude (Brändli 1998; Houston et al. 2016). This coincidence between the occurrence of *O. uncinata* and *P. sylvestris* is not restricted to Central Europe. It also applies to Scotland, where *O. uncinata* is closely associated with remnants of the ancient Caledonian Forest dominated by *P. sylvestris* and older pine plantations (Falks and Lewington 2015; Else and Edwards 2018), and probably even to the entire range of *O. uncinata*. In fact, almost all known records of *O. uncinata* fall neatly into the distribution of *P. sylvestris* as given by Caudullo et al. (2017). Possibly for climatic reasons, however, *O. uncinata* is absent from several southern regions, where relictual stands of *P. sylvestris* occur, such as northern Iberia, southeastern Europe, the Crimea, northern Turkey and the Caucasus. Interestingly, numerous records of *O. uncinata* in northwestern Germany, the Netherlands, Belgium and northern France lie outside the native range of *P. sylvestris* (Caudullo et al. 2017), suggesting a rather recent colonization after the widespread introduction and naturalization of this pine species all over western Europe during the last few centuries.

At higher altitudes above 1500 m a.s.l. in the subalpine zone of the Swiss Alps (Lötschental, Obergoms, Val Müstair) there exist a few reliable records of *O. uncinata* at localities where *P. sylvestris* does not occur. Dominant tree species at these localities are *Picea abies* (L.) Karsten, *Pinus cembra* L., *Pinus mugo* Turra and/or *Larix decidua*. Since the former three conifers have only a thin bark, they are unsuitable as nesting site for *O. uncinata*. In contrast, the bark of *L. decidua* is similar to that of *P. sylvestris* in both thickness and consistency. Therefore, we strongly assume that *O. uncinata* uses the bark of *L. decidua* as a substitute nesting substrate particularly at elevations above 1400 m a.s.l., where *P. sylvestris* becomes rare and *L. decidua* common (Brändli 1998). This assumption is supported by the discovery of several *O.uncinata* nests in *Larix* bark at 1630–1780 m a.s.l. in the Lötschental/Valais.

The pronounced preference of *O. uncinata* for thick-barked *P. sylvestris* trees appears to be the main factor determining the bee's habitat in Central Europe. Pines that are well exposed to sun and weather form particularly thick bark (A. Rigling, personal communication) possibly explaining why *O. uncinata* mainly occurs in open pine forests, along outer and inner forest edges dominated by pine or around isolated pine groups without any obvious clear preference for altitude, humidity or thermal conditions.

Conclusions

Osmia uncinata shows a patchy distribution in Central Europe due to its specialization to *Pinus sylvestris* stands, it usually occurs only in low population densities rendering it susceptible to local extinction, and it is red-listed in Switzer-

land, several German states and in Great Britain (Falk 1991; Amiet 1996; Scheuchl and Schwenninger 2015), which all call for measures to preserve and promote populations of this rare bee. The most promising measures are i) to augment the supply of suitable nesting sites by thinning pine stands to expose individual trees to direct sunlight or by liberating free-standing pines from adjacent shadowing shrubs or overhanging branches, and ii) to ensure a sufficient quantity of suitable pollen host plants in the vicinity of potential nesting sites, above all *Lotus* and *Hippocrepis* (Fabaceae).

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References

Amiet F (1996) Rote Liste der gefährdeten Bienen der Schweiz. In: Duelli P (Ed.) Rote Listen der gefährdeten Tierarten der Schweiz, BAFU, Bern, 38–44.

Bouwman BE (1922) Onze metselbijen (*Osmia*). De Levende Natuur 27: 86–93.

Brändli U-B (1998) Die häufigsten Waldbäume der Schweiz. Ergebnisse aus dem Landesforstinventar 1983–1985: Verbreitung, Standort und Häufigkeit von 30 Baumarten. Berichte der Eidgenössischen Forschungsanstalt für Wald, Schnee und Landschaft 342: 1–279.

Caudullo G, Welk E, San-Miguel-Ayanz J (2017) Chorological maps for the main European woody species. Data in Brief 12: 662–666. https://doi.org/10.1016/j.dib.2017.05.007

Correia MMDA (1981) Contribution à l'étude de la biologie d'*Heriades truncorum* (Hym., Apoidea, Megachilidae). III. Aspect éthologique. Apidologie 12: 221–256. https://doi.org/10.1051/apido:19810302

Danforth BN, Minckley RL, Neff JL (2019) The Solitary Bees – Biology, Evolution, Conservation. Princeton University Press, Princeton and Oxford, 472 pp. https://doi.org/10.2307/j.ctvd1c929

Edwards M (2001) Survey of Three Biodiversity Action Plan bee Species (*Colletes floralis*, *Osmia inermis*, *Osmia uncinata*) in Scotland, 2001. Unpublished report to the Scottish Natural Heritage (SNH) and the Royal Society for the Protection of Birds (RSPB), 18 pp.

Else G, Edwards M (1996) Observations on *Osmia inermis* (Zetterstedt) and *O. uncinata* Gerstäcker (Hym., Apidae) in the Central Scottish Highlands. Entomologists Monthly Magazine 132: 291–298.

Else GR, Edwards M (2018) Handbook of the Bees of the British Isles. Ray Society, London, 775 pp.

Falk SJ (1991) A review of the Scarce and Threatened Bees, Wasps and Ants of Great Britain. Research and Survey in Nature Conservation 35, Nature Conservancy Council, Peterborough.

Falks S, Lewington R (2015) Field Guide to the Bees of Great Britain and Ireland. Bloomsbury, London, 432 pp.

Forrest JRK, Cross R, CaraDonna PJ (2019) Two-year bee, or not two-year bee? How voltinism is affected by temperature and season length in a high-elevation solitary bee. The American Naturalist 193: 560–574. https://doi.org/10.1086/701826

Friese H (1891) Beiträge zur Biologie der solitären Blumenwespen (Apidae). Zoologisches Jahrbuch 5: 751–860.

Haeseler V (1982) Zur Bionomie der Küstendünen bewohnenden Biene *Osmia maritima* (Hymenoptera: Apoidea: Megachilidae). Zoologisches Jahrbuch für Systematik 109: 117–144.

Hawkins WA (1975) Nesting biology of *Osmia georgica* (Hymenoptera: Megachilidae). Journal of the Kansas Entomological Society 48: 493–499.

Houston D, de Rigo T, Caudullo G (2016) *Pinus sylvestris* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J et al. (Eds) European Atlas of Forest Tree species, Publication Office of the EU, Luxembourg, 131–133.

Ivanov SP, Fateryga AV (2018) Nesting biology of the bee *Hoplitis princeps* (Morawitz) (Hymenoptera, Megachilidae) in Crimea. Entomological Review 98: 995–1005. https://doi.org/10.1134/S0013873818080067

Le Goff G (2003) Une nidification verticale d'*Heriades truncorum* Linnaeus (Hymenoptera; Apoidea; Megachilidae; Osmiini). (Nouvel hôte pour *Chrysis ignita* L.). L'Entomologiste 59: 201–207.

Lemoine G (2016) Découverte d'*Osmia pilicornis* Smith, 1846 dans la Pévèle (région de Lille). Bulletin de la Société entomologique du Nord de la France 360: 9–13.

Minckley RL, Danforth BN (2019) Sources and frequency of brood loss in solitary bees. Apidologie 50: 515–525. https://doi.org/10.1007/s13592-019-00663-2

Müller A (1994) Die Bionomie der in leeren Schneckengehäusen nistenden Biene *Osmia spinulosa* (Kirby 1802) (Hymenoptera, Megachilidae). Veröffentlichungen für Naturschutz und Landschaftspflege Baden-Württemberg 68/69: 291–334.

Müller A (2018) Pollen host selection by predominantly alpine bee species of the genera *Andrena*, *Panurginus*, *Dufourea*, *Megachile*, *Hoplitis* and *Osmia* (Hymenoptera, Apoidea). Alpine Entomology 2: 101–113. https://doi.org/10.3897/alpento.2.29250

Müller A (2020) Palaearctic Osmiine Bees, ETH Zurich. http://blogs.ethz.ch/osmiini [accessed 5.1.2020]

Müller A, Prosi R, Praz C, Richter H (2019) Nesting in bark – the peculiar life history of the rare boreoalpine osmiine bee *Osmia* (*Melanosmia*) *nigriventris* (Hymenoptera, Megachilidae). Alpine Entomology 3: 105–119. https://doi.org/10.3897/alpento.3.34409

Müller A, Richter H (2018) Dual function of *Potentilla* (Rosaceae) in the life history of the rare boreoalpine osmiine bee *Hoplitis* (*Formicapis*) *robusta* (Hymenoptera, Megachilidae). Alpine Entomology 2: 139–147. https://doi.org/10.3897/alpento.2.30158

Packard AS (1868) The home of the bees. American Naturalist 1: 364–378. https://doi.org/10.1086/270104

Prosi R, Wiesbauer H, Müller A (2016) Distribution, biology and habitat of the rare European osmiine bee species *Osmia* (*Melanosmia*) *pilicornis* (Hymenoptera, Megachilidae, Osmiini). Journal of Hymenoptera Research 52: 1–36. https://doi.org/10.3897/jhr.52.10441

Raw A (1972) The biology of the solitary bee *Osmia rufa* (Megachilidae). Transactions of the Royal Entomological Society London 124: 213–229. https://doi.org/10.1111/j.1365-2311.1972.tb00364.x

Rightmyer MG, Griswold T, Arduser MS (2010) A review of the non-metallic *Osmia* (*Melanosmia*) found in North America, with additional notes on palearctic *Melanosmia* (Hymenoptera, Megachilidae). ZooKeys 60: 37–77. https://doi.org/10.3897/zookeys.60.484

Sakagami SF, Zucchi R (1978) Nests of *Hylaeus* (*Hylaeopsis*) *tricolor*: the first record of non-solitary life in colletid bees, with notes on communal and quasisocial colonies (Hymenoptera: Colletidae). Journal of the Kansas Entomological Society 51: 597–614.

Scheuchl E, Schwenninger HR (2015) Kritisches Verzeichnis und aktuelle Checkliste der Wildbienen Deutschlands (Hymenoptera, Anthophila) sowie Anmerkungen zur Gefährdung. Mitteilungen des Entomologischen Vereins Stuttgart 50: 3–225.

Sears J, Amphlett A, Macdonald M, Taylor S (2014) A survey of the mason bee *Osmia uncinata* in Caledonian pine woodlands and evaluation of its status in 2006-07. Scottish Natural Heritage Commissioned Report No. 784, 19 pp.

Stoeckhert FK (1933) Die Bienen Frankens (Hym. Apid.). Beiheft der Deutschen Entomologischen Zeitschrift 1932: 1–294.

Taylor S (2011) Evaluation of trap-nests for monitoring *Osmia uncinata* bees. Scottish Natural Heritage Commissioned Report No. 794, 7 pp.

Taylor S (2015) Firwood Cottage, Self-Catering, Accommodation, Nethybridge, Scotland, Highlands, Aviemore, Bird Watching, Wildlife. http://firwoodcottage.blogspot.com/2015/08/ and http://firwoodcottage.blogspot.com/2015/09/ [accessed 5.1.2020]

Tischendorf S (2002) Ergänzungen zur Stechimmenfauna (Hymenoptera, Aculeata) Hessens, I. Anhang. Jahrbücher des nassauischen Vereins für Naturkunde 123: 5–32.

Westrich P (2018) Die Wildbienen Deutschlands. Ulmer, Stuttgart, 821 pp.

Willems E (2010) Waarnemingen aan de Bosmetselbij (*Osmia uncinata*) te Malle. Nieuwsbrief sectie Hymenoptera van de Nederlandse Entomologische Vereniging 31: 37–38.

WSL (2019) Schweizerisches Landesforstinventar LFI. Daten der Erhebungen 1983/85 (LFI1), 1993/95 (LFI2), 2004/06 (LFI3) und 2009/16 (LFI4). Datenbankauszug vom 27.9.2019. Eidg. Forschungsanstalt WSL, Birmensdorf.

Supplementary material 1

List of distributional data of *Osmia uncinata*

Authors: Rainer Prosi, Andreas Müller

Data type: XLS file

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Link: https://doi.org/10.3897/alpento.4.53489.suppl1